Ecological Complexity 33 (2018) 57–65

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Original research article

Traveling waves and spatial patterns from dispersal on homogeneous and gradient habitats

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ARTICLE INFO

Article history:
Received 14 July 2017
Received in revised form 28 November 2017
Accepted 2 December 2017
Available online 8 December 2017

Keywords:
Agent based model
Dispersal
Ecotone
Environmental gradient
Traveling waves

ABSTRACT

Models of dispersal for response to global climate change can refer to theory on traveling waves developed for invasions. The relevance of this theory may depend on its density- versus habitat-dependence, but it has not considered environmental gradients nor related feedbacks. An agent based simulation model (ABM) for a plant species or vegetation type is developed here, focusing on properties of traveling waves. The ABM simulated no-tailed, thin-tailed, and fat-tailed dispersal kernels (random uniform, Gaussian, and Cauchy kernels, respectively). Probabilities were based on either population density or habitat, and for the latter as homogeneous or on a gradient, and if a gradient positive feedback from populations to the habitat was added to represent process at ecotones such as a positive feedback switch or the stress gradient hypothesis (SGH) feedback. The uniform and Gaussian kernels produced traveling waves with constant speed, but the fat-tailed Cauchy kernel produced traveling waves that accelerated and also flattened as the low-probability portion of wave accelerated fastest. On a gradient, when populations approached the limit of habitability the waves steepened and stopped traveling. The effect of SGH feedback on traveling wave slopes depends on the dispersal kernel. With strong facilitation on the gradient, greater variety of spatial patterns were able to develop among the replicate simulations of the fat-tailed kernel when it flattened to a greater spatial extent of low probability presence. In addition to the heterogeneity of the habitat and its modification by facilitation, the details of dispersal can also affect the feedback between spatial pattern and the establishment process that will affect the rate of advance of a species or an ecotone into new territory.

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1. Introduction

1.1. Ecological response to climate change

The migration of species is the primary response of species to climate change as seen during the past 20,000 years. Migration in response to ongoing and future climate change has been modeled in various ways (Pitelka, 1997; Thuiller et al., 2008; Travis et al., 2013; Ferrarini et al., 2014). Although the importance of spatial processes have long been recognized (e.g., Hanson et al., 1989), many models are not sufficiently spatially explicit (among other simplifications; cf. Ferrarini et al., 2017). Statistical species distribution models, mechanistic models, and their occasional combination usually do not include the process of dispersal across or into landscapes of varying habitat or do so phenomenologically (Heikkinen et al., 2006; Cabral et al., 2017). The primary reason for this shortfall is weak parameterization of dispersal kernels. The tails of the kernels determine the spatial process, but these tails, representing long distance dispersal, are difficult if not impossible to determine empirically (Horn et al., 2001; Bullock et al., 2017). Some mathematical models using reaction-diffusion equations skip over the step of creating dispersal kernels and instead imbed a diffusion rate (Leroux et al., 2013). Theoretically, however, dispersal kernels from jump processes, as opposed to birth-jump processes studied here, are relatively well understood (e.g., Bates et al., 1997; Coville, 2007; Berestycki et al., 2009) and are background to other ecological processes (e.g., Banerjee and Volpert, 2017).

New research is exploring various elements of the dispersal process contribution to response to climate change (Garcia and Borda-de-Agua, 2017). We aim to develop a narrative on how

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https://doi.org/10.1016/j.ecocom.2017.12.001
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dispersal kernels might affect the advance of a species, and an ecotone, on an environmental gradient.

Ecotones are the focus of much research on responses to ongoing climate change: in forest-savanna (Staver et al., 2011; Oliveras and Malhi, 2016), forest-grassland (Whitesides and Bekker, 2011; Dee and Palmer, 2017) and forest-tundra (Dullinger et al., 2004; Malanson et al., 2011; Boisvert-Marsh et al., 2014; Camarero et al., 2017) among others. At such boundaries the spatial patterns appear to be in a feedback loop with processes (Harsch and Bader, 2011), but linkage is problematic. Malanson and Zeng (2004) found that a model with evolutionary algorithms quickly converged on patterns from different initial conditions. Zeng and Malanson (2006) developed a model-based narrative of advance-coalescence-advance for alpine treeline ecotones in which spatial advances were linearly associated with spatial patterns created by nonlinear feedbacks; they described the result as a self-organized system. Bourgeron et al. (2015) described similar patterns as multiscalar. The problem has the hallmarks of nonlinear complexity (Loehle et al., 1996; Malanson, 1999; Li, 2002; Burkett et al., 2005).

Attention has focused on these contrasts because it is likely that biotic interactions, competition and/or facilitation, could occur. The related conceptual frameworks of a positive feedback switch (Wilson and Agnew, 1992) and the stress gradient hypothesis (SGH) (Maestre et al., 2009) have developed and been applied to such ecotones. The positive feedback or facilitation that would occur at the advancing ecotone of a biome should increase its rate of advance, but this advance is dependent on the continually changing spatial pattern. Other work has emphasized the spatial nature of the facilitation (e.g., Malanson 1997; Malanson and Resler, 2015; Malanson et al., 2017), but competition is an alternative (e.g., Hernandez-Garcia et al., 2015). These relations have consequences for the continued existence of species, the diversity of areas at multiple scales, ecosystem function, and resulting ecosystem services. Most work has focused on the heterogeneity of the abiotic environment as the source of spatial pattern (e.g., Holtmeier, 2003; Resler et al., 2005; Butler et al., 2007; Elliott and Cowell, 2015) or on the spatial feedback, including directional effects (e.g., Alftine and Malanson, 2004; Smith et al., 2003; Bader et al., 2008). Some have suggested that evolving spatial patterns at ecotones could be interpreted through the lens of complexity theory (Malanson, 1999; Mills et al., 2006; Zeng and Malanson, 2006).

These and other studies of feedback between spatial patterns and ecotones have not adequately addressed the role of dispersal (but see Brooker et al., 2007; Ferrarini et al., 2014), although the pattern of seedling recruitment is sometimes observed (Rehm and Feeley, 2013; Johnson et al., 2017). For the movement of a species or an ecotone, dispersal is a prerequisite. We follow a line of modeling initiated by Kot (1992) and expanded, critiqued, and reiterated by Kot et al. (1996, 2004) and Clark et al. (2001), with new insights from Potapov and Lewis (2004) that led to the recent work by Leroux et al. (2013). In these papers Kot and colleagues found that the advance of a species into new territory could accelerate, but acknowledged that in extremis this would be unrealistic. Clark et al. (2001); Clark Lewis et al., 2003 proposed biological restrictions that would lead to non-accelerating advances. Kot et al. (2004) faulted this approach (somewhat cryptically) for including density dependence. While seeming to apply only to general constraints, the assessment of traveling waves remains a useful approach, however, because they remain a link between more generalizable formal theory and landscape-specific applications models. Most of that work addressed the ecological issue of invasion of an area by a new species; therein, the habitat of the area was homogenous for the species. Others have addressed dispersal in the advance of a species or biome in the context of climate change; therein, the habitat could be a gradient, otherwise heterogeneous, and/or changing (Malanson and Armstrong, 1996; Malanson, 1997; Malanson and Cairns, 1997; He and Mladenoff, 1999; Lischke et al., 2006).

1.2. Traveling waves

A related literature on advancing biological fronts has also examined traveling waves. Observation and modeling of traveling waves of expanding patterns of bacteria in Petri dishes have considered sharp waves (Kawasaki et al., 1997; Satnoianu et al., 2001; Mansour, 2008; Jalbert and Eberl (2014). Normally, the waves studied have some regularity (usually continuously differentiable) and are strictly positive in the domain. However, sharp waves have an abrupt limit at the low-probability end and are exactly equal to zero in parts of the domain.

Generally, these patterns have been modeled with reaction-diffusion equations rather than a birth-jump dispersal process. However, recently *birth-jump processes* have been introduced to describe a population or trait for which dispersal cannot be decoupled from birth. These types of models were introduced recently (Hillen et al., 2015}) as a generalization to integro-differential equations that arise from a *position-jump process* (a stochastic process that generalizes random walks (Hutson and Martinez 2003; Othmer et al., 1988) in that individuals can make spatial jumps with a given probability) and reaction-diffusion equations (Cantrell and Cosner, 2003).

Motivated by these studies, Rodriguez and Malanson, 2017(Rodriguez and Malanson, in review), however, introduced a birth-jump processes leading to a degenerate reaction-diffusion equation (in the diffusion-limit), which produced sharp waves. Working in parallel, here we develop an agent based simulation to explore some details of traveling waves. Beyond demonstrating their existence, however, we begin consideration of their consequences for spatial pattern-process feedbacks. We examine traveling waves that arise from differences in specific density-versus environmental-dependence, dispersal kernels, and environmental gradients, with and without positive feedback. Although motivated by outcomes in PDE Rodriguez and Malanson, 2017(Rodriguez and Malanson, in review), those are not a prerequisite. We use agent based simulation models (ABM) because it allows realistic spatially explicit representation of these processes and constraints (some of which were noted by Lewis and Pacala, 2000). ABM are a group of models that focus on individuals and derive from models created for practical application, not theoretical development (Grimm and Railsback, 2005). In their most extended form, agent based models have been used to examine the interactions of individuals responding to climate change across complicated landscapes (Dey et al., 2017; Redmond et al., 2017) and in more abstract or stylized scenarios (Smith-McKenna et al., 2014; Mohd et al., 2016). However, theory can be explored using ABM, at some cost of tradeoff of ABM strengths (e.g. Malanson, 2015).

1.3. Questions addressed

We asked: Can traveling waves represent the relevant processes? Do waves have characteristic shapes? Do waves accelerate, and under what circumstances? We also search for conditions that would give rise to, or approximate, distributions for sharp waves.

We hypothesize:

- Traveling waves produced from density-dependent seed production do not differ qualitatively from those produced from

habitat dependent seed production (density will be a function of habitat).
- Fatter tails will lead to faster advance and acceleration of the traveling wave, and the slope extend (as reported by Kot et al., 1996).
- An environmental gradient will lead to slower advance, deceleration, and steepening slope of the traveling wave (although rate changes are trivial expectations, steepening is a consequence of the area of high probability occupancy catching up with that of low probability as a species or ecotone advances on a gradient).
- The addition of positive feedback to an advance will not affect the rate of advance but will steepen the slope of the traveling wave (positive feedback only affects immediate neighborhood, which creates a more abrupt habitat change).

Beginning with a birth-jump model Rodriguez and Malanson, 2017(Rodriguez and Malanson, in review), we developed a spatially explicit agent based simulation to investigate the effects of four factors that they did not consider: density vs. environmental dependence, dispersal kernels, and environmental gradients with and without stress gradient feedback. We interpret the traveling waves as representing either a single species or an ecotone.

2. Methods

2.1. Agent based simulation

To put the basic birth-jump model into and agent based simulation, we created a one-dimensional grid, i.e. a transect, of length 7000 (long enough that processes were unconstrained). We initialized the simulation with 10 individuals on each of the first 20 cells at one end of the transect. Each extant individual or location was subject to a probability of reproduction; the offspring dispersed on the transect and then was subject to a probability of establishment; all individuals could be subject to a probability of mortality, but here we set mortality at zero for simplicity; mortality induces slight stochasticity and reduces source strength and rate of advance – but qualitative results are unchanged.

2.1.1. Environmental gradient and stress gradient feedback

For environmental gradients we include no gradient, with all locations having the same habitat multiplier, here 0.5, for births, establishment, and death, and a linear gradient from 1 to 0 in the direction of the advance (i.e., as with climate change, the advance is into less-habitable places). The steepness of the gradient was tuned for the dispersal kernels so that the leading edges of the populations began to be impinged at (reached habitat < 0.5) at the same point in time. These gradients were:

$$H_{xu} = 1 - 0.0025\times \quad (2)$$

$$H_{xg} = 1 - 0.002\times \quad (3)$$

$$H_{xc} = 1 - 0.000333\times \quad (4)$$

where H is the habitat multiplier for x distance along the transect for the uniform u, Gaussian g, and Cauchy c, kernels. For example, all reached the $H = 0.5$ at about 250 iterations.

We also included a representation of the SGH. The SGH states that interaction among neighbors will change along a gradient of abiotic environmental stress. Interactions would be largely competitive/negative at low stress/high productivity and largely facilitative/positive at high stress/low productivity (Maestre et al., 2009). How the change in interaction plays out along observed environmental gradients is varied, and this switch in sign can be defined and modeled in various ways (e.g., Malanson and Resler 2015, 2016; Malanson, 2015). We used a simple representation in which interaction strength increases with the number of occupied cells, j, in a 3-cell neighborhood (as 10j/3) and this interaction is multiplied by a function, S, of the habitat H, with a curve fitted so that multiplier S is 0.5 at $H = 1$, 1 at $H = 0.5$, and 2 at $H = 0$ so that

$$S = 2\, e^{-1.386H} \quad (5)$$

This multiplicative approach anchored the point where the habitat viability is zero and did not advance it farther on the gradient.

2.1.2. Habitat and density bases

We compared two approaches for modeling the probability that an individual or location will create a seed:

$$P_{bh} = 1 - e^{-h_x} \quad (6)$$

$$P_{bn} = 1 - e^{-n_x} \quad (7)$$

Where P_{bh} is the probability of seed production by each individual at location x with habitat h, P_{bn} is the probability of seed production the cell at location x with population density n. The latter is completely density dependent and embodies an Allee effect because the probability of reproduction increases non-linearly with population.

2.1.3. Dispersal kernels

For dispersal kernels we examined a null or no-tail kernel, a thin-tail kernel, and a fat-tail kernel. Many studies indicate that fat-tailed kernels are often at play and long distance dispersal (LDD) is common, but non-LDD also occurs (Bullock et al., 2017). Here, we implemented a uniform random distance within a limit, a Gaussian distribution, and a Cauchy distribution. The uniform, Gaussian, and Cauchy distributions are what we might expect for limited home range animal dispersal, gravity dispersal (i.e., minimal wind), and wind or long-distance animal dispersal, respectively. Other kernels could be used, but these capture the major differences (cf. Kot et al., 2004). The distances were calculated separately for each seed using these computations:

$$D_u = \text{random number, 0–50} \quad (8)$$

(9) D_g = Gaussian random number, mean 0 and standard deviation σ

$$D_c = \sqrt{(((\gamma^2/r) * \pi * \gamma) - \gamma^2)} \quad (10)$$

where r is a floating point random number, 0–1. In the simulation the parameters are tuned so that the mean distance is the same, an arbitrary 25 cells, in all cases ($\sigma = 31.3$; $\gamma = 3.7$)

2.1.4. Carrying capacity and establishment

Environmental and density dependence both operate in all cases at the establishment phase. After jump dispersal, the probability of establishment is the product of the habitat and a Verhulst logistic equation with carrying capacity 10 (chosen to manage computational intensity; this limit thus includes some density dependence at this point):

$$P_e = H_x - nH_x/10 \quad (11)$$

The carrying capacity of 10 was arbitrary. With dispersal and establishment linked for agents, no partial individuals were created (Clark Lewis et al., 2003 critique of deterministic models).

2.1.5. Search for sharp traveling waves

To search for sharp waves we examined another difference in dispersal with six simulations. We cut tails of distributions. Clark et al. (2001) argued that a problem with accelerating waves was that the tails were not bounded while the planet, and more reasonably continents, are of finite size. Cutting tails has been shown to affect outcomes in ecological models wherein dispersal was one of several processes (Malanson and Armstrong, 1996). For the Gaussian kernel, we stopped dispersal beyond 0.9 σ or beyond 1.1 σ. We chose 0.9σ and 1.1σ so that the points were on either side of the concave-convex inflection point of the Gaussian curve. These cutoff points produced average distances that were 75% and 83% of the mean dispersal distance, respectively; we tuned dispersal to these same distances for the uniform and Cauchy kernels. For those seeds that would have gone farther, we applied three rules: they were eliminated, they bounced back a random distance toward their origin, or they landed at this cutoff point.

2.2. Simulation runs

The factors simulated were: gradients (binary), habitat or density basis, and the three dispersal kernels. To these 12 combinations we added the scenario in the search for a sharp traveling wave. We iterated the simulation 500 time steps for most scenarios, but for the gradient scenarios we extended this to 1500 steps. Most of the 13 combinations were replicated1000 times, but to reduce computational demand the Cauchy kernels and the 1500 iteration runs were repeated 100 times. The results were used to

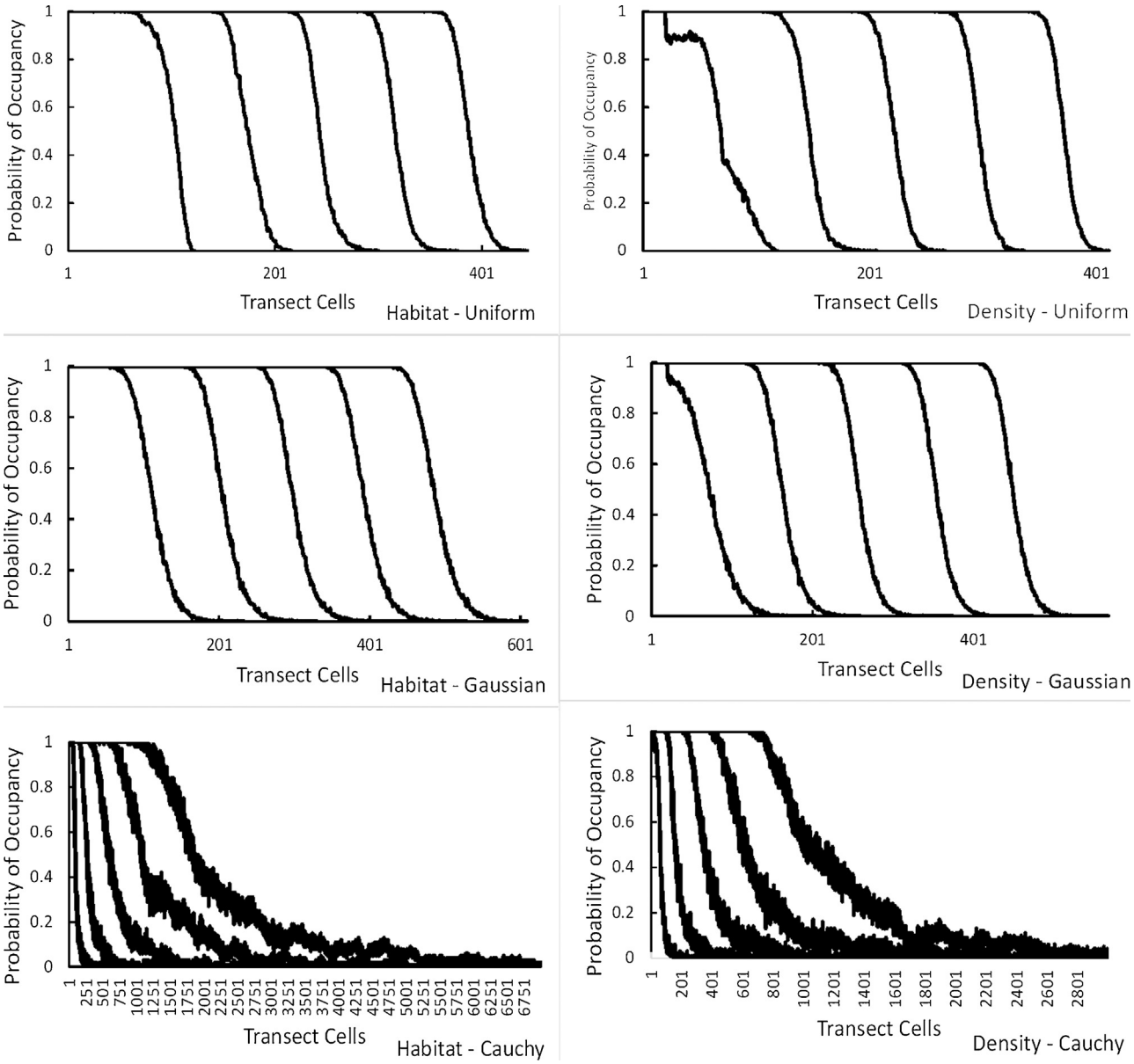

Fig. 1. Traveling waves on an environmental gradient from habitat-based and density-based functions for birth probability and three dispersal kernels. The left to right sequence in each graph show waves at 100, 200, 300, 400, and 500 iterations.

compute traveling waves of the probability that a grid cell will be reached per iteration. These traveling waves were then examined for their rate of advance and shape. At 100-iteration intervals we recorded the number of cells that the wavefront reached at which the probability of 0.50 as an indication of its speed for the habitat-based simulations with and without a gradient.

2.3. Spatial patterns

For the simulations we computed four metrics of spatial pattern during the first 500 iterations in order to examine their transient dynamics as might occur during an initial response (e.g., to climate change). We focused on the area of the transect that would comprise an ecotone – that between the lowest numbered unoccupied cell and the farthest occupied cell. We computed:

Extent – the distance between these two cells;

Edges – the number of unoccupied/occupied cell boundaries;

Edge density – the number of Edges relative to the Extent;

Singles – the number of occupied cells bounded by unoccupied cells on both sides.

These metrics are indicative of spatial complexity, given that the simulation is of a 1-D transect. Extent indicates how abrupt an ecotone might be and is a constraint on how complex patterns could develop. Edges and Singles indicate points where facilitation can effectively change the potential of the landscape to change.

We followed these simulations with examples in which we expanded the transect into two dimensions to illustrate the spatial pattern; we expanded to a width of 40 cells but the grid is horizontally wrapped into a cylinder so that there are no edges. We created visualizations of the patterns generated.

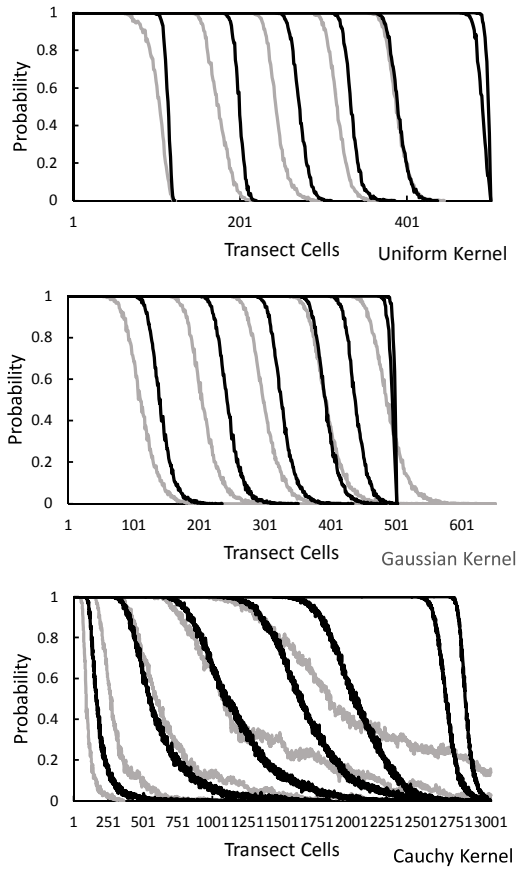

Fig. 2. Traveling waves on an environmental gradient (black) overlain on those of the homogeneous environment (gray; from Fig. 1, left panels) and three dispersal kernels. The left to right sequence in each graph show waves at 100, 200, 300, 400, 500, (both),1000 and 1500 (gradient only) iterations.

3. Results

3.1. Traveling waves

The traveling waves produced by the simulations for the two foundations, habitat-dependent and density, are shown in Fig. 1 for the three kernels (uniform, Gaussian, Cauchy) with a homogeneous environment. In Fig. 2 the waves for environmental gradient scenarios, with the additional waves at 1000 and 1500 iterations, are overlain on the habitat-based results from the left panel of Fig. 1.

3.2. Habitat vs. density bases

The habitat-based and density-based functions for birth probability produced similar traveling waves (Fig. 1, left and right panels, respectively). In the ABM framework, density dependence per cell only changed the base number of parents and thus slightly slowed an advance. The greater variability with the Cauchy kernel is almost entirely due to it greater variation in how far a given seed travels, not to fewer replications.

3.3. Dispersal kernels

The differences among the kernels were as expected. However, an aspect of the fat tailed kernel traveling waves is that while they accelerated, they also became flatter as the low-probability incidences accelerated fastest (Figs. 1 and 2, Table 1).

3.4. Environmental gradient and SGH feedback

The inclusion of an environmental gradient caused the traveling waves to slow and eventually stop as the limit of possible occupancy was approached (after 1000–1500 time steps (Fig. 2). With the uniform and Gaussian kernels, as the waves approached the limit of advance they became visually less distinguishable from sharp waves, but remained sigmoidal. The Cauchy kernel maintained more of a sigmoidal shape (even with more time steps) because of the greater stochasticity in its tail. For all three scenarios, the rate of advance was faster initially with an environmental gradient, when $H_x > 0.5$, but slowed thereafter (Table 1). As H_x decreased, the wavefronts became steeper; this reversed the flattening trend for the Cauchy kernel while it simply steepened the otherwise constant slopes of the no-gradient waves for the other kernels. In the limit, all would become vertical fronts.

In the scenarios of uniform and Gaussian kernels with an environmental gradient, the traveling waves not only slowed – they changed shape. They began to lose their low-probability extensions. This result gives rise to the possibility of degenerate functions or functions of compact support, or at least observations could be fit with such functions. This type of sharp wave has been discussed for contagiously spreading bacteria in a petri dish (Kawasaki et al., 1997; Satnoianu et al., 2001; Mansour 2008; Jalbert and Eberl, 2014), but not previously for any jump dispersal process.

In the cases with SGH, the feedback increased the rate of wave propagation but then brought the wave up against the limit of the environmental gradient (Fig. 3). As in the gradient cases, the wave steepened and began to give the illusion of a sharp wave as the limit was approached. With the Cauchy kernel, in the intermediate iterations the wave became even flatter than in earlier scenarios as the low-probability events accelerated toward the limit.

Table 1
The average speed (cells/iteration) for the three dispersal kernels on the transects with (w) and without (n) an environmental gradient (as in Fig. 2).

Kernel/ Gradient	→100	→200	→300	→400	→500	→1000	→1500
U/n	0.96	0.61	0.66	0.66	0.65		
U/w	1.15	0.85	0.72	0.62	0.66	0.20	0.01
G/n	1.12	0.91	0.93	0.94	0.93		
G/w	1.43	1.11	0.97	0.85	0.73	0.34	0.05
C/n	1.35	2.65	3.55	4.59	5.72		
C/w	1.68	4.38	7.58	9.50	9.10	4.93	1.12

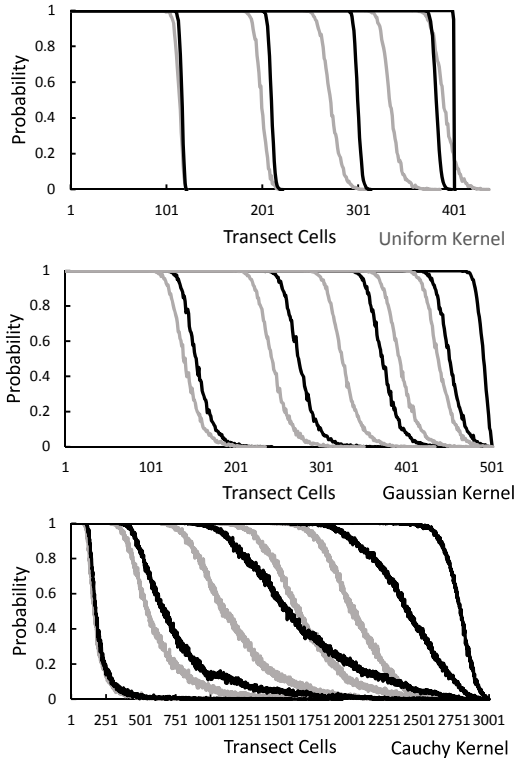

Fig. 3. Traveling waves on an environmental gradient with stress gradient hypothesis positive feedback (black) and without feedback (gray; as in Fig. 2, black there) and three dispersal kernels. The left to right sequence in each graph show waves at 100, 200, 300, 400, 500 iterations.

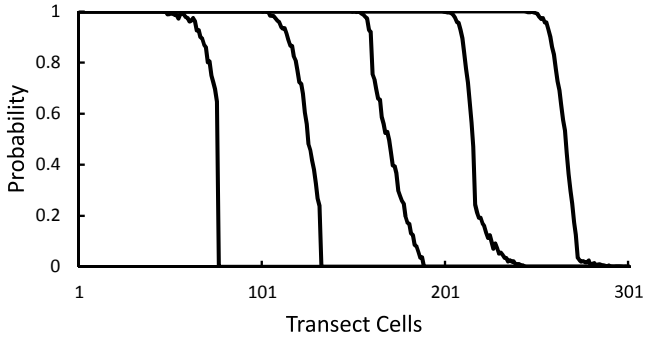

Fig. 4. Waves visually similar to sharp waves appeared at 100–300 iterations for a case when dispersal is limited to $<\sigma$ in the Gaussian kernel.

3.5. Sharp traveling waves?

In our additional trials, one instance produced what appeared to be sharp waves in apparent response to compact support; they are not, however formally sharp waves. In the case with the cutoff at 0.9 s in the Gaussian kernel and where the seeds that would have gone farther landed at that point, an apparently sharp wave was formed – but even then only for a limited period (iterations 100–200) during which the probability of occupancy reached mid-levels and then dropped to zero at farther distances along the transect (Fig. 4).

Table 2
Mean and coefficient of variation of the four spatial metrics indicative of potential complexity in the ecotone; extent – rows in simulation between contiguous cell occupancy and most advanced individual; edges – number of unoccupied cells among 4 neighbors for all occupied cells; edge density – edges/extent; singles – occupied cells with no occupied neighbors.

Metric/Kernel	Uniform	Gaussian	Cauchy
Extent	47.46	68.63	506.25
CV	0.922	0.683	0.918
Edges	14.92	19.63	48.95
CV	0.28	0.283	0.529
Edge density	0.374	0.318	0.158
CV	0.284	0.284	0.634
Singles	2.91	4.57	13.13
CV	0.602	0.484	0.709

3.6. Spatial pattern in 2-D

Additional consequences of the changing waves on the environmental gradient were changes in the spatial pattern (Table 2). With the fat tailed Cauchy kernel, the broader spatial extent of low probability occurrence implies patchiness as seen in more edges and single-cell patches. In two dimensions, most of the dispersed spatial pattern was in the form of individuals without neighbors (Fig. 5). However, the density of edges and individuals within the extent of the ecotone is greater with the Gaussian and uniform kernels because more broad, unoccupied areas exist within the greater extent. When we added the feedback of the stress gradient hypothesis, the pattern developed into larger patches.

4. Discussion

4.1. Traveling waves

The core results rehearse what was expected from previous studies: First, the uselessness of average distances has long been recognized; most of eastern Canada would still be treeless if mean dispersal distances events were separated by generation times (e.g., Malanson and Cairns, 1997). Second, fat-tailed kernels produce faster traveling waves than did thin tailed kernels, which in turn are faster than uniform kernels with the same average distance. Third, fat-tailed kernels produce accelerating waves – in our case even with density dependence and whole-number agents.

A salient result is that with a fat-tailed kernel the traveling waves not only accelerate but flatten. The lowest probability, most advanced cells occupied in this scenario were increasingly farther ahead of the definitely—occupied cells. The ecotone was extended,

Fig. 5. Generalized spatial pattern (the vertical dimension shows the 47, 69, and 506 rows of the ecotones) of occupied cells at 500 iterations from the uniform (U), Gaussian (G), and Cauchy (C) kernels for simulations with a stress gradient feedback.

and spatial patterns differed. While spatial patterns per se may be of interest, positive feedback to either seed production or establishment from extant individuals is a pathway by which spatial pattern affects the spatial process such as the rate of advance (Zeng and Malanson 2006; Harsch and Bader 2011; Camarero et al., 2017).

The effects of a gradient and SGH, not included in previous studies of traveling waves nor in some of the more mathematical formulations of advances following climate change (Leroux et al., 2013), were more complicated than expected. The SGH feedback did increase the speed of the waves in all cases. The amount of difference was not expected because the feedback was focused only on adjacent cells. Over enough iterations, the effect is apparent. The SGH feedback did steepen the traveling waves once they reached the area of lower habitat quality where it became effective. The effect of SGH feedback on traveling wave slopes depends on the dispersal kernel: increasing the width of the tail from none-to-thin-to-fat has the effect of flattening the waves in the middle iterations before the waves run up against the limit on the gradient (noting that in our SGH multiplicative implementation the limit was constant; an additive implementation could move the limit). With no tail (uniform kernel), the waves steepened when the SGH feedback was added; with the thin tails (Gaussian kernel) the waves shape remained the same; with the fat tails (Cauchy kernel) the waves flattened strongly in the middle iterations. Where the leading low probability establishment of the Cauchy kernel occurred it was amplified by the SGH feedback.

The flatter waves with the feedback-enhanced low probability establishment events gave rise to varied spatial patterns, including patches (a literature on tree islands for arctic and alpine treelines exists; cf. Resler et al., 2005; Albertsen et al., 2014). With the fat-tailed Cauchy dispersal kernel on the environmental gradient with strong stress gradient feedback, the spatial pattern of the advance changes trough time. Instances of individual LDD become focal points for the development of larger patches. Because these events are rare, they occur at different times and places among the replicate simulations, and are not fully captured by averaged spatial statistics.

At this point we do not see sharp traveling waves and so cannot take advantage of new insights into stability properties they determine Rodriguez and Malanson, 2017(Rodriguez and Malanson, in review).

4.2. Spatial patterns

Different dispersal kernels can lead to different spatial patterns of a species moving into a new range, and thus of an ecotone advancing on an environmental gradient. Our simulations indicate that a wide variety of spatial patterns can develop for fat-tailed dispersal kernels given enough time and space on an environmental gradient. With a stress gradient hypothesis effect, more edges create more potential for facilitation to affect the dynamics. Fat-tailed kernels create a broader ecotone within which spatial patterns can develop. Individual simulation runs, as indicated in Fig. 5, seem to replicate the advance-coalescence-advance sequence modeled by Zeng and Malanson (2006), but this spatiotemporal pattern cannot develop in the compressed ecotones produced by the thinner-tailed kernels.

Sharp waves imply little low probability establishment in front of the advancing core population. Thus they would create simple spatial patterns that could be more predictable in terms of their feedbacks and overall rate of advance.

Combined with environmental heterogeneity and variation in feedback strength and direction almost any observed spatial pattern, and possibly others, could develop from similar underlying processes (cf. Cale et al., 1989); alternatively, the increased

extent could allow the development of self-organized complexity that might be seen in spatial patterns (cf. Zeng and Malanson, 2006). Differences in dispersal kernels, even within fat-tailed ones, could alone create different patterns given that patterns are time- and distance-dependent. Combinations of factors: kernels, feedback strengths, environmental heterogeneity, density dependence, and biotic interactions will create variation in traveling waves and so in patterns and rates of advance of ecotones in responses to global change. Future interaction between stochastic partial differential equation modeling and ABM should be able to map these aspects of response onto those factors.

5. Conclusions

From the study of ecotones, a consensus is emerging on the complexity of spatial responses to climate change. This consensus recognizes the amplification of climate change at microclimate level by positive feedback or facilitation processes (from the positive feedback switch hypothesis (Wilson and Agnew, 1992) and the more general stress gradient hypothesis (Malanson et al., 2017). These processes will respond to the spatial pattern and density of individuals, which in turn result from dispersal and establishment processes. While establishment is part of the feedback, dispersal kernels may be more independent (except where the dispersal process is itself linked to the spatial pattern as might be the case with wind dispersal or mutualistic animal dispersal; cf. Brooker et al., 2007). Dispersal provides an additional dimension that creates greater complexity in the response of ecotones to climate change.

Rodriguez and Malanson, 2017(Rodriguez and Malanson, in review), working in parallel on PDEs, were able to demonstrate sharp traveling waves, derive several theorems, and analyze stability. We found waves close in form to sharp waves but only in a limited (and probably ecologically unrealistic) context. The dialectic with this work here, however, enables further examination of the details of traveling waves (noting the cautionary outlook of Lewis and Pacala, 2000, but following Rodriguez and Bertozzi, 2010, Rodriguez, 2015). These may go beyond demonstrating their existence to consideration of feedbacks between their shapes and the processes that create them. Whether this approach is able to capture the feedback associated with complex spatial patterns is yet to be determined.

Acknowledgments

This work was supported by grant DMS-1516778 from the National Science Foundation to NR.

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